ON THE RESPIRATORY FUNCTION OF THE BLOOD OF THE PORPOISE

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THE WOODS HOLE OCEANOGRAPHIC INSTITUTION [1]

The capture of two porpoises, *Phocæna phocæna* Linn., in the fish trap operated by the Marine Biological Laboratory has afforded an opportunity to obtain data which have not been available before on the conditions of equilibrium between the blood of a cetacean and the respiratory gases. The mammals of this order are so strikingly modified morphologically in adaptation to their aquatic life that an examination of the physico-chemical properties of the respiratory fluids is attended with some interest. While the results recorded in the present paper require confirmation and extension in many details, the general picture of the physico-chemical system involved in transporting the respiratory gases is sufficiently definite to warrant presentation in the present provisional form.

The porpoises were brought from the trap on May 14 and placed in a large floating crate at the laboratory. One died on the following day and was used to determine the proper approach for cardiac puncture. The other lived until May 18, when it was killed in the course of experiment. During this period it lay in the water rather quietly and did not struggle when held. On May 17 fifty cubic centimeters of blood was drawn by puncture of the left ventricle, the needle being inserted one inch behind and above the caudal edge of the left flipper. The porpoise did not struggle. A 10 cc. portion of this blood was preserved under oil, for the determination of the carbon dioxide content of arterial blood. The remainder was used for the determination of the shape of the oxygen and carbon dioxide dissociation curves. Coagulation was prevented by the use of dry sodium oxalate. The blood drawn at this time will be designated *Specimen A*.

The following day an unsuccessful attempt was made to measure the blood volume by the vital red method. Twenty cubic centimeters of blood were drawn from the heart with some difficulty and it appeared that both right and left ventricles had been pierced as a portion of the sample was not fully oxygenated. This sample was oxalated and used for the determination of oxygen capacity and cell volume and was designated *Specimen B*.

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Immediately after drawing Specimen *B*, the porpoise went into asphyxial convulsions, evidently as the result of cardiac failure. The thorax was opened and 50 cc. of blood were drawn directly from the ventricle. This sample was designated as *Specimen C* and was used for determining the effect of hydrogen ion concentration upon the position of the oxygen dissociation curve.

Methods

Oxygen and carbon dioxide contents were determined by using the Van Slyke constant volume analyzer. The gas mixtures were analyzed with a Haldane apparatus after equilibration and the pressures calculated by means of the equation developed by Bock, Field, and Adair (see Henderson, 1928, p. 384). The blood was equilibrated with the gas

Table I

Oxygen Capacity and Volume of Erythrocytes in the Blood of Aquatic Mammals

Species	Porpoise Phocæna phocæna			Dolphin Tursiops tursio	Sperm Whale Physeter macrocephalus	Sea Lion Eumetopias stelleri
Specimen	A	B	C			
Oxygen capacity, vol. per cent	22.15 22.20	19.8 19.7	20.44 20.34			19.8
Oxygen combined, vol. per cent	21.78	19.35	19.99	31.8	29.09	19.4
Volume of cells in 1 cc. blood, cc	0.35	0.35	0.36	0.517		0.29
Oxygen combined in 100 cc. cells, vol. per cent	62.2	55.4	55.6	61.5		67

mixtures at 38°, preserved in blood-sampling tubes over mercury, and promptly analyzed. The original specimens of blood were preserved in the refrigerator until used, and all measurements were made within twenty-four hours of the time the specimens were secured.

The Oxygen Capacity of the Blood and of the Erythrocytes

Table I contains the data obtained from the three specimens of blood we have examined, together with results reported by Jolyet (1902) for the dolphin and sperm whale, and by Florkin and Redfield (1931) for the sea lion. The oxygen capacities we obtained, like those observed in the sea lion, are of the same magnitude as those commonly found in terrestrial mammals. They contrast strongly with the higher values recorded by Jolyet and Sellier (1896–97) for the porpoise (30.9 volumes

per cent), by Jolyet (1902) for the dolphin and sperm whale, and with the values of 42.5 and 45.1 volumes per cent reported by Sudzuki (1924) for the blood of porpoises. Whether these differences are characteristic of the different species in question, or are due to accidental causes, such as a possible anæmic condition of the individuals yielding the lower values, or to experimental errors, cannot be decided until more data are available. We were impressed with the rapidity with which the corpuscles settled out when the porpoise blood was allowed to stand and believe that errors large enough to account for the differences reported for the different species might readily arise from this cause were it not guarded against. The observations are all in agreement in showing that a given volume of the corpuscles of these aquatic mammals combines more oxygen than does an equal volume of

TABLE II

Data on carbon dioxide equilibrium in porpoise blood. Temperature, 38° C.

	Oxygen pressure	Carbon dioxide pressure	Carbon dioxide content
	mm. Hg	*mm. Hg*	*vol. per cent*
Specimen A	150 ca.	30.7	35.8
	150 ca.	51.3	46.0 46.2
Specimen C	150 ca.	41.0	25.6 25.5
	150 ca.	51.1	29.7 29.0
	1.4	51.8	32.45 32.30

corpuscles of the terrestrial mammals, in which 100 cc. of corpuscles have an oxygen capacity of about 45 cc.

THE CARBON DIOXIDE DISSOCIATION CURVE

Table II records the data obtained by equilibrating Specimens *A* and *C* with carbon dioxide. From these data the carbon dioxide dissociation curves illustrated in Fig. 1 have been constructed by making use of the approximation (Henderson, Bock, Dill, and Edwards, 1930):

$$\log T = A \log (p\mathrm{CO}_2) + B,$$

in which T is the total carbon dioxide content of the blood, A and B are constants, and pCO_2 is the carbon dioxide pressure. The curve constructed from data on Specimen A does not differ greatly from that of normal man, though the carbon dioxide combined at any pressure is somewhat less. The curve for Specimen C represents blood drawn following death from asphyxia, and the combined carbon dioxide is consequently less at each carbon dioxide pressure.

These curves may be used for comparing the buffer action of porpoise blood with that of human blood. Henderson, Bock, Dill, and Edwards (1930) have prepared a nomogram showing the relation between the slope of the carbon dioxide dissociation curve, its height, and the hemoglobin content of human blood based on an examination of

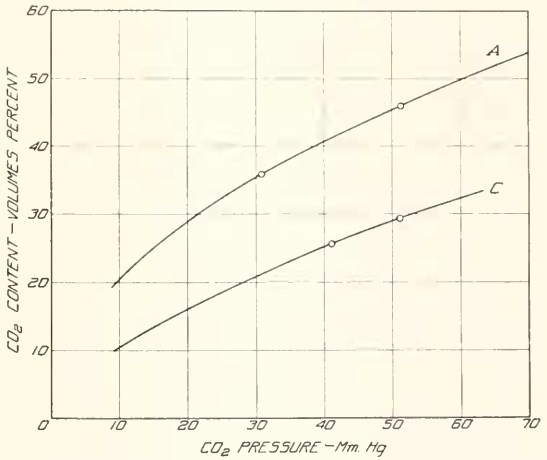

Fig. 1. Carbon dioxide curve of blood of porpoise. Upper curve, Specimen A. Lower curve, Specimen C. For data see Table II.

some 117 specimens. In Table III are recorded the values of Hb, the hemoglobin content as measured by oxygen capacity; T_{40}, the carbon dioxide content at 40 mm. carbon dioxide pressure; and Δ, the difference in carbon dioxide content at 30 and 60 mm. carbon dioxide pressure as deduced from the curves and data describing Specimens A and C. In this table are also recorded the values of Δ characteristic of human blood having equivalent values for Hb and T_{40}, taken from the nomogram of these authors. Both specimens of porpoise blood have slightly higher values of Δ than does comparable human blood. The differences, however, are not greater than might be accounted for by experimental error. Comparable data for the blood of the sea lion, from the measurements of Florkin and Redfield (1931), and mean

values for dog blood given by Dill, Edwards, Florkin, and Campbell (1932) are included in the table. The comparison serves to emphasize the similarity of the bloods when regarded as systems for transporting carbon dioxide.

Table II contains measurements of the carbon dioxide content of a sample of Specimen *C* equilibrated with carbon dioxide in the virtual absence of oxygen. Comparing the results with the value obtained from the curve in Fig. 1 for the same carbon dioxide pressure, it appears that the reduced blood combines about 2.86 volumes per cent more carbon dioxide than does oxygenated blood. This effect is similar to that observed in other mammalian bloods but is rather smaller than usual for blood of comparable oxygen capacity.

TABLE III

Comparison of Buffer Value of Oxygenated Porpoise and Sea Lion Blood with that of Man

Species	*Hb* Oxygen capacity	T_{40} CO_2 content at pCO_2 = 40 mm.	Δ observed	$T_{60} - T_{30}$ calculated from human blood	Ratio
	milliequiv. per liter	*milliequiv. per liter*	*milliequiv. per liter*	*milliequiv. per liter*	
Porpoise					
Specimen A	9.73	18.18	6.52	5.80	1.12
Specimen C	8.93	11.22	5.12	4.70	1.09
Sea Lion	8.88	16.02	5.32	5.30	1.00
Dog (Mean)	9.7	18.1	5.78	5.76	1.00

THE OXYGEN EQUILIBRIUM

Data on the equilibrium of Specimen *A* with oxygen are presented in Table IV. In order to fit the measurements, the oxygen dissociation curve shown in Fig. 2 was drawn using Hill's equation

$$y = \frac{Kx^n}{1 + Kx^n} \times 100,$$

in which y is the percentage saturation of the hemoglobin, x the oxygen pressure, $K = 0.00102$ and $n = 2.1$. The carbon dioxide pressure of these samples was about 46.5, corresponding to a carbon dioxide content of 44 volumes per cent. Taking $pK = 6.14$, yields a value for pH of 7.29. The values for n which have been used to characterize the blood of man vary from 2.2 to 2.5. The shape of the oxygen dissociation curve of the porpoise so far as it is characterized by n does not differ markedly from human blood.

The portion of Specimen *A* which was collected under oil had a carbon dioxide content of 45 volumes per cent, corresponding to a carbon dioxide pressure of 49 mm. and a pH of 7.27. Consequently the oxygen dissociation curve in Fig. 2 represents approximately the conditions characteristic of the blood *in vivo*, if one neglects the change in oxygen

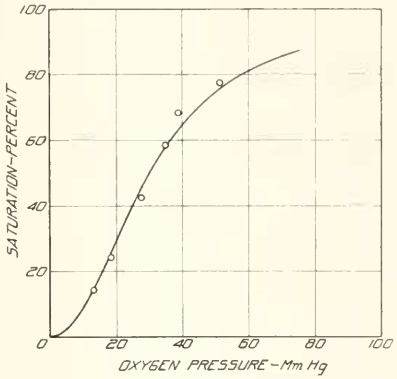

FIG. 2. Oxygen dissociation curve of blood of porpoise at a carbon dioxide pressure of approximately 46 mm.—equivalent to that of arterial blood. For data see Table IV.

equilibrium, due to the increased carbon dioxide content of the venous blood.

THE EFFECT OF HYDROGEN ION CONCENTRATION ON THE OXYGEN DISSOCIATION CURVE

Table V contains data for the oxygen equilibrium of samples of Specimen *C* obtained at a variety of carbon dioxide pressures. Using

TABLE IV

Data on the equilibrium of oxygen with porpoise blood, Specimen A.
Temperature, 38° C.

Carbon dioxide pressure	Oxygen pressure	Oxygen content	Oxygen dissolved	Oxygen as oxyhemoglobin	Saturation
mm. Hg	*mm. Hg*	*vol. per cent*	*vol. per cent*	*vol. per cent*	*per cent*
46.5	13.0	3.14	0.03	3.11	14.3
46.4	18.1	5.30	0.05	5.25	24.1
46.6	27.5	9.37	0.07	9.28	42.5
47.2	34.9	12.86	0.09	12.77	58.6
38.7	38.7	14.95	0.12	14.83	68.1
42.7	51.4	16.98	0.15	16.83	77.3
air	air	22.18	0.40	21.78	100.0

Hill's equation and taking the value of $n = 2.1$, the values of K, and of p_{50} (the oxygen tension at which the blood would be half saturated with oxygen) have been calculated. As an empirical procedure this practice involves only the assumption that the form of the oxygen dissociation curve, determined by the value of n, remains unchanged at various carbon dioxide tensions. This assumption is amply justified by the behavior of other mammalian hemoglobins. The hydrogen ion concentration of the various samples have also been calculated with the aid of the

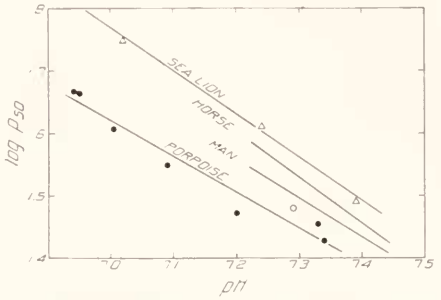

FIG. 3. Relation of p_{50}, the oxygen tension at which blood is half saturated, and the pH of the serum of whole blood. For data see Table V and references in text. Hollow circle, porpoise Specimen *A*. Solid circles, porpoise Specimen *C*.

carbon dioxide dissociation curve for Specimen *C* in Fig. 1. From these values the relation between p_{50} and pH shown in Fig. 3 has been plotted.

For precise comparison of the properties of hemoglobin in the blood of different animals the properties should be referred to the pH of the cell contents. Unfortunately our studies did not include the measurements necessary to enable us to calculate this value. We have conse-

TABLE V

Data on the equilibrium of oxygen with porpoise blood (Specimen C) at different carbon dioxide tensions. Temperature, 38° C.

Carbon dioxide pressure	Oxygen pressure	Saturation	log p_{50} calc.	pH
mm. Hg	*mm. Hg*	*per cent*		
9.86	34.4	62.7	1.428	7.34
10.5	23.5	40.0	1.455	7.33
21.4	18.4	26.7	1.473	7.20
39.7	27.1	36.3	1.550	7.09
52.5	45.1	56.5	1.607	7.04
87.6	38.9	41.2	1.664	6.95
92.0	54.4	58.3	1.666	6.94

quently compared the values of p_{50} obtained at different carbon dioxide pressures with those characterizing other bloods when the pH of the serum of the whole blood was the same. This comparison is included in Fig. 3, the data for the horse and for man being taken from the nomograms given by Henderson (1928); that for the sea lion is calculated from the data of Florkin and Redfield (1931). When compared on this basis the hemoglobin of the porpoise does not differ strikingly from that of other mammals and does not differ from the blood of normal man much more than the blood of men differ from one another.

Discussion

The preceding observations all tend to indicate that the general physico-chemical properties of the blood of the porpoise are very similar to those of the terrestrial mammals. Even in the strictly quantitative aspects of the various properties of the blood one can detect very little variation from the mean conditions observed in human blood. The increased concentration of hemoglobin in the corpuscles of the cetaceans and the sea lion is perhaps the only clear-cut condition which might be regarded as an adaptation to the more rigorous respiratory requirements of aquatic life.

Unfortunately, our attempts to determine the blood volume of the porpoise were unsuccessful. This relation is, in our opinion, the most important aspect of the respiratory mechanism which remains to be examined. One cannot help being struck by the richness of the muscular tissue in hemoglobin. It seems probable that in this condition, and perhaps in other modifications of the chemical situation in the muscles, adaptations to aquatic life may be found.

It should be pointed out that the porpoise is not in the habit of remaining submerged for long periods of time when compared to the larger Cetacea and certain other aquatic mammals. Parker (1932) records that in a porpoise confined in a large tank, the average respiratory interval was 15.48 seconds. The shortest interval observed was 6.5 seconds, the longest 31.7 seconds. These are not strikingly greater than the intervals of inspiration in man and might easily be maintained, at least temporarily, by voluntary effort in his case. When feeding in the open sea, one might expect the intervals to be greater and Jolyet and Kükenthal (quoted by Parker) note that dolphins may remain under water much longer, Jolyet setting the maximum at about fifteen minutes. The general testimony of whalers indicates that the larger Cetacea are in the habit of remaining submerged for much longer periods. Whether more distinct adaptations of the physico-chemical mechanisms of the blood will be found in such forms remains to be seen.

Summary

The properties of the blood of the porpoise, *Phocæna phocæna*, considered as a system for the transport of oxygen and carbon dioxide, have been examined.

It does not appear that the morphological changes adapting these animals for aquatic life are accompanied by significant modifications in the physico-chemical properties of the blood.

The only striking characteristic of porpoise blood, when compared with that of terrestrial mammals, is an increased concentration of hemoglobin in the corpuscles.

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